Differential effect of luminance contrast reduction and

noise on motion induction

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Hanada, M. (2010) Differential effect of luminance contrast reduction and noise on motion induction.

Perception, 39(11), 1452-1465.

Abstract

Motion perception in a region is affected by motion in the surround regions. When a physically static or flickering stimulus surrounded by moving stimuli appears to move in the direction opposite to that of the surround motion, it is referred to as motion contrast. When the center appears to move in the same direction, it is referred to as motion assimilation. We investigated how noise and luminance contrast affects motion induction by employing static and dynamic counterphase flickering targets. The tendency of motion assimilation was found to be stronger at a high noise level than at a low noise level for both static and dynamic targets. On the other hand, a decrease of luminance contrast tended to strengthen the tendency of motion contrast. However, the addition of noise and the decrease of luminance contrast decreased the visibility of motion comparably. These results suggest that the visual system changes the mode of motion induction according to the noise level, but not the visibility.

1. Introduction

Perception of an object's motion is affected by the motion of surrounding objects. If a static object is surrounded by objects moving in a particular direction, the central static object generally appears to move in the opposite direction (Duncker 1929; Over and Lovegrove 1973; Levi and Schor 1984; Muragami and Shomojo, 1996). This is called motion contrast. In some situations, however, the central object appears to move in the direction of the surround motion. This is called motion assimilation. For example, when surrounding sinusoidal gratings are displaced by a 90-deg phase and a center grating is simultaneously displaced by a 180-deg phase (the contrast polarity of the center grating is reversed), the center grating appears to move in the same direction as the surround gratings (Ido et al 1997; Ohtani et al 1995). Nawrot and Sekuler (1990) reported that cinematograms comprised of alternating strips cause motion assimilation under some conditions; for narrow stripes, randomly moving dots in one stripe appear to move in the same direction as the moving dots in the adjacent stripes.

One of the important factors in determining the perceived direction of induced motion is stimulus size. When the target is small, motion assimilation tends to occur, and When the target is large, motion contrast tends to occur (Nawrot and Sekuler 1990; Murakami and Shimojo 1993, 1996). The size effect can be explained by center-surround antagonistic motion processing units, which consist of an excitatory area surrounded by a suppressive area. When stimulus size is small, both central and peripheral stimuli lie in the central excitatory area. Hence, the motion units are excited by peripheral motion, and motion assimilation occurs. In contrast, when the stimulus size is moderately large, the induced central stimulus lies in the central excitatory area of some motion units, and the peripheral inducing stimulus lies in the inhibitory area. Since the motion units are inhibited by the peripheral motion, it would be thought that motion contrast should occur. However, several studies have shown that motion assimilation and motion contrast occurs in the same spatial configuration (Ido et al 1997; Ido et al 2000; Hanada 2004). These results suggest that the occurrence of motion contrast and motion assimilation cannot be explained solely by fixed center-surround motion receptive fields.

When an induced luminance grating is stationary, motion contrast usually occurs and motion assimilation does not (e.g., Ido et al 1997). Motion assimilation often occurs when the induced stimulus is dynamic noise or ambiguous motion (Chang and Julesz 1984; Nawrot and Sekuler 1990; Murakami and Shimojo 1996). Motion assimilation tends to occur when the inducing motion is jerky, whereas motion contrast is apt to occur when the inducing stimuli move smoothly (Ohtani et al 1995; Ido et al 1997, 2000). Motion assimilation occurs when induced dots are isoluminant color-defined or when the luminance contrast of induced dots is low (Ramachandran 1987; Murakami and Shimojo 1993). These results suggest that when noise is large or when a signal is weak, motion assimilation tends to arise, and motion contrast is apt to occur when noise is small. In our previous study (Hanada 2004), we hypothesized that as the SNR (signal to noise ratio) decreases, the mode of motion induction changes from motion contrast to motion assimilation. The adaptation according to SNR would increase the transmission of information about motion signal. Information transmission is increased by additively integrating nearby signals to collect information in a large area for low SNR, and by differentiating nearby signals to reduce redundancy for high SNR (Barlow et al. 1957; Atick, 1992; van Hateren, 1993). We tested the hypothesis by examining the effect of the noise level on motion induction, and found that motion contrast occurs at a low noise level, while motion assimilation arises at a high noise level (Hanada 2004).

Recently, it has been reported that luminance contrast also affects surround inhibition in motion processing. Tadin et al (2003) measured duration and phase-step thresholds of a moving grating for direction discrimination as a function of stimulus size and luminance contrast. They found that duration and phase-step thresholds for motion stimuli increase with an increase of stimulus size at high luminance contrast, and decreases with it at low luminance contrast. Tadin and Lappin (2005) measured the optimal size for motion discrimination varying levels of luminance contrast, and reported that the optimal size increased as the luminance contrast decreased. These results can be explained as an adaptive change of surround suppression in motion processing as a function of luminance contrast; surround suppression is stronger at high luminance contrast than at low luminance contrast. At high luminance contrast, large stimuli stimulate surround regions, which should inhibit activity and impair performance. At low luminance contrast, large stimuli stimulate expanded excitatory regions, which should enhance the response of motion processing units. Tadin et al (2003) also examined the effect of noise, and found that reduction of luminance contrast and increase of noise have similar effects. This suggests that the visibility (or SNR) is the critical factor in the adaptive change of surround

suppression. In addition, Paffen et al (2006) reported that a decrease of luminance contrast weakened surround suppression in motion processing during binocular rivalry. They dichoptically presented rival grating targets moving in opposite directions. Each target was surrounded by a grating moving in the same direction as one of the targets. The predominance of the target matched to the surround decreased at high luminance contrast, and increased at low luminance contrast.

A number of physiological studies also reported the adaptive change of the receptive field with luminance contrast. MT(V5) in the cortex has neurons that respond to stimuli moving in one direction. The activities of some neurons in MT are inhibited by surrounding stimuli moving in the same direction and enhanced by those moving in the opposite direction (Allman et al 1985; Tanaka et al 1986; Born and Tootell 1992). Pack et al (2005) reported that the decrease of luminance contrast tends to expand the excitatory region in MT neurons. In addition, V1 contains neurons that respond to moving stimuli, and are inhibited by stimuli moving in the same direction outside the classical receptive field. Cavanaugh et al (2002) reported that the inhibition of V1 cells due to surround stimulation reduced with a decrease in luminance contrast.

If center-surround integration is the cause of motion induction due to surround motion, evidence from the physiological and psychophysical studies reported above would predict that the reduction of luminance contrast should increase the tendency of motion assimilation.

However, there is some room for doubt about the hypothesis that surround inhibition

weakens for low-contrast moving stimuli. Some methodological issues have been raised concerning the effects of contrast and size found by Tadin et al (2003). Churan et al (2009) measured phase-step thresholds for direction discrimination as Tadin et al (2003), with a brief delay from the stimulus onset to the onset of motion. They found that the effect of stimulus size at high luminance contrast disappeared when the delay was larger than 120 msec. They suggested that the masking effect of sudden stimulus onset explains the size effect on direction discrimination at high luminance contrast. Furthermore, Aaen-Stockdale et al (2009) showed that paradoxical effects of contrast and size found by Tadin et al (2003) can be explained by low-level mechanisms without surround suppression. Having normalized the stimuli relative to contrast threshold, Aaen-Stockdale et al (2009) showed that the effects of contrast and size can be entirely explained by the relative contrast of the stimulus. Recently, however, Glasser and Tadin (2010) presented experimental results that cannot be explained by the relative contrast. Since they used short presentation time, however, there is a possibility that their results will be explained by the masking effect as suggested by Churan et al (2009).

Only the noise level was manipulated in Hanada (2004), and whether decrease of luminance contrast affects motion induction in the same way as do changes in noise remains unknown. In this study, we examined the effects of luminance contrast as well as the noise level on motion induction. In an earlier study I used temporally varying noise (dynamic noise) (Hanada 2004). Noise can also be static (temporally unchanged), and static noise might not have the same effect on motion induction. In this study I used both static and dynamic noise.

2. Methods

Apparatus. Stimuli were generated by a visual stimulus generator ViSaGe (Cambridge Research Systems Ltd.). This apparatus can display 256 colors through R, G, and B channels, each of which has 14-bit DAC. Stimuli were displayed on a color CRT display. The viewing distance was 60 cm. The refresh rate of the display was 80 Hz. The display size was 1024 pixels \times 768 pixels, subtending 29 deg \times 22 deg. Observers binocularly viewed the display in a dark room with their head supported by a chin rest.

Observers. Six observers participated in this experiment. One was the author, the others were undergraduate students who were unaware of the purpose of the experiment. All the observers had normal or corrected-to-normal acuity.

Stimuli. The stimuli consisted of a central part and a surround, as shown in figure 1. The radius of the center region was 1.5 deg, and the surround annulus spanned from 1.5 deg to 5.1 deg. The background luminance was 40 cd m⁻² as was the average luminance of the center and surround gratings. The surround grating moved smoothly leftward or rightward. The central part was the target grating. Two types of targets were used: counterphase flickering grating (the dynamic target) and static grating (the static target). Motion induction due to the surround motion was measured as the motion intensity of the target required to cancel induced motion. The motion intensity for the static target was controlled by changing velocity; the target grating was moved slowly to cancel motion induction. Positive and negative velocities indicate leftward and

rightward motion, respectively. The motion intensity of a counterphase-flickering grating for the dynamic target was controlled as follows. The counterphase-flickering grating is decomposed into two sinusoidal gratings moving in opposite directions. The directional bias of the target can be controlled by changing the luminance contrast of the two components. The luminance profile of the target grating at the image point (x, y) and at the time of *t* was

$$L(x, y, t) = L_{mean} \left[1 + r c \sin\left\{ 2\pi (f x + \omega t) + \theta \right\} - (1 - r) c \sin\left\{ 2\pi (f x - \omega t) + \theta \right\} \right]$$
(1)

where L_{mean} denotes the mean luminance of the grating (the same as the background luminance), *c* denotes the luminance contrast, *r* is a parameter for controlling the relative strength of the leftward and rightward moving gratings, and *f* and ω are the spatial and temporal frequencies. *r*=0.5 means the counterphase flickering; values more than 0.5 indicate leftward motion bias; and values smaller than 0.5 indicate rightward motion bias. Motion intensity for the dynamic target was controlled by varying the value of *r*. The temporal frequency of the central grating was 1.0 Hz. The parameters for the standard stimulus were as follows. The spatial frequency of the target and surround gratings was 1.0 cycledeg⁻¹. The luminance contrast of the target and the surround was 0.25 (Michelson). The temporal frequency of the surround drifting grating was 4.0 Hz. No noise was added to either the target or the surround for the standard stimuli. The target was either counterphase-flickering (dynamic target) or static (static target).

Three types of stimuli were produced by modifying the standard stimulus. (i) dynamic noise

was added to both target and surround (dynamic noise); (ii) static noise was added to both target and surround (static noise); (iii) the luminance Michelson contrast of the target and the surround was reduced to 0.025 (low luminance contrast). For (i) and (ii) above, vertical line noise was added to the center and surround gratings. The value for each vertical line noise was randomly determined from the uniform distribution between $-0.75 \times L_{mean}$ to $0.75 \times L_{mean}$. The vertically-uniform, horizontally-varying random noise was generated for one cycle of the center and surround gratings, respectively. The noise was repeated for the stimulus width, following which it was added to the gratings. The noise pattern was updated at each frame for dynamic noise, but not for static noise. Static noise was stationary relative to the display, and did not move. Examples of the standard and noise stimuli are shown in figure 1.

Figure 1: Insert Figure 1 about here.

Procedure. In a trial, a stimulus was presented for 1.0 s. After the presentation, the observers indicated the apparent direction of the target grating presented in the central region by pressing an appropriate button. Two experimental factors were varied within a session: motion direction of the surrounding grating (left or right) and motion bias for the target (the value of r for the dynamic target or velocity for the static target.). 15 values of r around 0.5 or the target velocity around 0 were used to obtain psychometric functions. Hence, there were 2×15 conditions within a session. There were 10 trials for each condition, producing a total of 300 trials in a

session.

There were eight stimulus conditions, which were varied between sessions: the standard stimulus and three variations (dynamic noise, static noise, low luminance contrast) for both the dynamic and static targets. The observers participated in two sessions for each between-session condition.

Each observer participated in practice sessions prior to the experimental trials. The range of r or the target velocity for each condition was determined from the results of the practice sessions for each observer.

3. Results

Figure 2a shows the percentage of "left" responses (P_{left}) as a function of r in the dynamic target condition of the standard stimulus for an observer. There were more "left" responses for the rightward moving surround than for the leftward moving one around r = 0.5. This indicated that motion contrast occurred for the standard stimulus. Figure 2b shows the psychometric functions of the same observer for the dynamic target in the dynamic noise condition. This observer responded "left" more for the rightward moving surround grating than for the leftward moving one around r = 0.5. Thus, motion assimilation occurred in the dynamic noise condition.

Figure 2: Insert Figure 2 about here.

Figure 2c shows the percentage of "left" responses as a function of target velocity in the static target condition of the standard stimulus for another observer. There were also a greater number of "left" responses for the rightward moving surround grating than for the leftward moving one around a velocity of 0. Thus, motion contrast also occurred for the static target of the standard stimulus. The psychometric functions for the static target in the static noise condition are shown in figure 2d. This figure indicates slight motion assimilation; the observer responded "left" more often for the rightward moving inducer than for the leftward moving one.

The Logit analysis was used to fit the following logistic function into the data for each condition of each observer.

$$P_{left} = \frac{1}{1 + \exp(-\alpha(x - \beta))} \times 100 \quad [\%]$$
 (2)

where α and β represent the slope and the uncertainty point (the point at which the percentage of the "left" responses would be 50%), and *x* denotes *r* in equation (1) for the dynamic target or the target velocity for the static target. We estimated the values of the two parameters (α and β) by the maximum likelihood method. We define "motion induction index" I as

$$I = \beta_r - \beta_l \qquad (3)$$

where β_l and β_r denote the uncertainty points for the inducers moving leftward and rightward,

respectively. The motion induction index implies signed shift of the psychometric function for the rightward moving inducer from that for the leftward moving one. A negative value indicates motion contrast and a positive one implies motion assimilation. The motion induction indices for the dynamic and static targets are shown in figure 3 and 4, respectively.

Figure 3: Insert Figure 3 about here.

Figure 4: Insert Figure 4 about here.

The motion induction indices for the dynamic noise stimuli are shown in figure 3a and 4a. For both static and dynamic targets, the motion induction indices were larger for the dynamic noise stimulus than for the standard stimulus. This indicates that dynamic noise increased the tendency of motion assimilation.

The effect of static noise on the motion induction index is shown in figure 3b and 4b. Static noise also increased the motion induction index except for observer KY in the dynamic target condition. Static noise eliminated the tendency of motion contrast, and changed the mode of motion induction to motion assimilation.

The effect of luminance contrast on the motion induction index is shown in figure 3c and 4c. Luminance contrast reduction decreased the motion induction indices for the dynamic target except for observer KY. For the static target, the motion induction indices slightly decreased for four out of the six observers. A decrease of luminance contrast somewhat strengthened the tendency of motion contrast.

Two one-way repeated-measure ANOVAs was used to compare the means for the four stimulus conditions (standard, dynamic noise, static noise and low luminance contrast) on the motion induction index, separately for the dynamic and static targets. The main effect was significant for the dynamic target (F(3, 15) = 6.2, p < .001) and for the static target (F(3, 15) = 6.2, p < .001)16.0, p < .001). An a posteriori analysis by Ryan's method (Ryan 1959) showed that, for the dynamic target, the differences between dynamic noise and low luminance contrast, and between static noise and low luminance contrast were significant (p < .05). However, the difference between dynamic noise and static noise was not significant, and those between the standard and the other conditions were not significant at the 0.05 level. For the static target, there were significant differences between static noise and low luminance contrast, and between dynamic noise and low luminance contrast (p < .05), whereas the difference between dynamic noise and static noise was not significant. The differences between standard and dynamic noise, between standard and static noise were significant (p < .05), but the difference between and standard and low luminance contrast was not significant. Although the statistical power seems to be insufficient to show significant differences between standard and the other stimuli for the dynamic target, the analyses clearly show that the effects of luminance contrast reduction on motion induction were different from those of dynamic and static noise.

SNR, or the visibility of motion, was manipulated by varying the noise level and the luminance contrast. The slope of a psychometric function is an index of performance for motion

direction discrimination. The visibility of motion should be reflected by the slope. The averages of the estimated slopes [α in equation (2)) for the leftward and rightward inducers are shown in figure 5. They were smaller (shallower) for static and dynamic noise than for the standard stimulus. There was little difference between the conditions of static noise, dynamic noise, and low luminance contrast. Thus, the addition of noise and the decrease of luminance contrast reduced the visibility of motion to a similar extent.

Figure 5: Insert Figure 5 about here.

One-way repeated-measure ANOVAs with the four stimulus conditions on the slope were conducted separately for the dynamic and static targets. The main effect was significant for the dynamic target (F(5, 25) = 23.3, p < .001) and for the static target (F(5, 25) = 11.90, p < .001). An a posteriori analysis by Ryan's method showed that for both static and dynamic targets, the differences between standard and dynamic noise, between standard and low luminance contrast, and between standard and static noise were significant (p < .05). The differences between dynamic noise and low luminance contrast, between static noise and low luminance contrast, and between dynamic noise and static noise did not reach the significance level. Thus, the statistical analyses did not support significant differences in visibility between low luminance contrast, dynamic noise, and static noise.

4. Discussion

In this study, the effect of luminance contrast in addition to noise was examined, and the differential effects of noise and luminance contrast reduction on motion induction were found; noise strengthened the tendency of motion assimilation, whereas luminance contrast reduction had little effect on motion induction. Since the reduction of luminance contrast decreased discrimination performance in the same manner as the noise addition did (see Fig. 5), the SNRs in both cases would be comparably low. Hence, the mode of motion induction does not necessarily depend on visibility or SNR. Noise addition and luminance contrast reduction have often been used to measure discrimination or detection thresholds in the study of motion perception. The differential effects of luminance contrast reduction and noise imply that the integration of local motion signals for stimuli at low luminance contrast is different from that of noisy stimuli. Noise addition could not be used as an alternative to control of luminance contrast in experiments on motion perception.

There were fairly large individual differences in baseline motion induction index for standard stimuli; motion induction indices for some observers were positive and for other observers were negative. Large individual differences in motion induction for dynamic target were also reported by Nishida et al (1997). Since their results suggest that the individual differences are larger when temporal frequency is lower for the inducer than for the target, I used higher temporal frequency for the inducer than for the target. However, this setting was not sufficient to eliminate the individual differences in the baseline motion induction index. It should be noted, however, that noise effect on motion induction was robust even when there were large individual differences in baseline motion induction.

A difference in visibility does not explain the difference in motion induction between the stimulus conditions within individual observers. However, it might explain the individual differences in baseline motion induction indices. Therefore, I examined relation of motion induction indices in the standard condition and visibility (slope of psychometric functions). The correlation coefficients between individual motion induction indices and individual slopes of psychometric function was small (r=0.16 for the static target and r=0.07 for the dynamic target) and not statistically significant. Hence, visibility does not explain individual differences in the baseline motion induction index. This result also supported the view that the mode of induction index is not determined by visibility.

In my previous study (Hanada 2004), I reported the same noise effect on motion induction using slightly different stimuli. In that study, stimuli consisting of three rows of vertical gratings were used. The upper and lower gratings were inducers, and the central one was the counterphase flickering target. Only temporally changing dynamic noise was used. In the present study, a circular grating and an annular surround were used as the center and the surround. Both a static target and a dynamic one were employed. Also, static noise was used in addition to dynamic noise. The tendency toward motion assimilation was strengthened by the addition of noise to both static and dynamic targets, regardless of whether noise was dynamic or static. Thus, the effect of noise on motion induction is robust with regard to stimulus configurations and the temporal properties of the target.

In this study, the noise was added to both center and surround. In my previous study (Hanada 2004), however, the noise levels of center and surround were varied separately in an experiment. Noise in the surround as well as in the center was found to strengthen the tendency of motion assimilation. The result suggests that the overall noise level affects center-surround interaction in motion. Since in my previous study I found the same effect of noise in both centre and surround, addition of noise to both should not present a problem.

Center-surround interaction in motion processing has also been examined in other psychophysical paradigms. Tadin et al (2003) showed that duration thresholds for motion direction discrimination increased with increasing stimulus size and luminance contrast. The results suggest that surround inhibition in motion processing weakens with a decrease of luminance contrast. Paffen et al (2006) reported that surround inhibition disappeared during binocular rivalry at low luminance contrast. On the other hand, the results of this study suggest that surround inhibition does not weaken at low luminance contrasts. Difference in luminance contrast at low luminance contrast might account for the discrepancy in reports of the effects of luminance contrast on center-surround interaction. In the present study, 2.5% luminance contrast was used, whereas Paffen et al (2006) employed 1.5% contrast. Tadin et al (2003) used 2.8% as their lowest luminance contrast for Gabor patches; however, the contrast of the peripheral part was much lower. Luminance contrast lower than 2.5 % could weaken surround suppression. The disappearance or decrease of surround suppression was reported at luminance contrast higher

than 2.5 %; however, this was the case only for random-dot stimuli (Tadin et al 2003; Tadin and Lappin 2005; Paffen et al 2006).

I conducted an additional experiment with luminance contrast less than 2.5%. Four different observers and the author participated in this experiment. Four kinds of stimulus conditions were employed. (i) Standard, (ii) Dynamic noise, iii) 1.5 % luminance contrast, and iv) 1.0% luminance contrast. The motion induction indices obtained in this additional experiment are shown in Fig. 6. A decrease of luminance contrast to 1.5% or 1.0% clearly strengthened the tendency of motion contrast, while the dynamic noise increased that of motion assimilation¹. The slopes of the psychometric function are shown in Fig. 7. The slopes were smaller for 1.0% luminance contrast than for dynamic noise, though the difference was not statistically

¹ One-way repeated-measure ANOVAs with the four stimulus conditions on the motion induction index in Fig. 6 were conducted separately for the dynamic and static targets. The main effect was significant for the dynamic target (F(3, 12) = 16.6, p < .001) and for the static target (F(3, 12) = 7.7, p < .01). An posteriori analysis by Ryan's method showed that for the dynamic target, the differences between dynamic noise and 1.5% luminance contrast, as well as between dynamic noise and 1.0% luminance contrast were significant (p < .05) for the dynamic target. For the static target, the difference between dynamic noise and 1.0% luminance contrast was significant (p < .05), but the difference between dynamic noise and 1.5% luminance contrast was not significant at the 5% significance level. Although the statistical power for five observers was not enough to obtain the significant difference between dynamic noise and 1.5% luminance contrast reduction on motion induction were different from those of dynamic noise.

significant². The visibility was definitely not higher for the 1.0%-contrast condition than for the noise condition. The results exclude the possibility that luminance contrast in this study were not low enough to erase surround suppression.

Figure 6: Insert Figure 6 about here.

Figure 7: Insert Figure 7 about here.

Thus, the discrepancy in luminance contrast effects on center-surround interaction between Tadin et al (2003) or Paffen (2006) should not be attributed to the difference in luminance contrast. However, there are other potential reasons than luminance contrast for the discrepancy. For stimuli, Tadin et al (2003) used one unified Gabor patch. Although the stimulus size was varied, the center and peripheral regions were not separated. Integration of local motion signals might be different for the separated center and surround gratings, and the unified Gabor patch. However, since the stimulus used in Paffen et al (2006) had distinct center and surround parts,

² One-way repeated-measure ANOVAs were also conducted on the slope in Fig. 7 separately for the dynamic and static targets. The main effect was significant for the dynamic target (F(3, 12) = 30.6, p < .001) and for the static target (F(3, 12) = 32.4, p < .001). However, the differences between dynamic noise and 1.5% low luminance contrast, and between dynamic noise and 1.0% low luminance contrast were not significant at the 5% significance level for the dynamic and static targets. The statistical analyses show that the visibility for 1.0% and 1.5% contrast was not higher than that for dynamic noise.

the discrepancy between their results and this study cannot be explained by the difference in stimulus configuration. Although their stimuli were similar to those employed in this study, there are differences in the stimulus such as stimulus size, spatial and temporal frequencies for component gratings. Since Paffen et al. (2006) used binocular rivalry to examine center-surround interaction, not only spatial interaction in motion but also interocular suppression should be reflected on their results. These differences might affect spatial interaction in motion. Further studies are needed to resolve the discrepancy. Whatever the reasons for the discrepant results between Tadin et al (2003) or Paffen et al (2006) and this study, the results presented in this paper indicate that surround inhibition does not necessarily weaken or disappear at low luminance contrast. The contention of Tadin et al (2003) that surround inhibition in motion weakens at low contrast or at low visibility does not hold for at least some stimulus conditions. This study showed that there are some stimulus conditions in which fairly large surround inhibition arises in motion at low contrast. Moreover, the results in this study imply that noise has more influence on center-surround interaction in motion than luminance contrast. Thus, not only luminance contrast but also noise should be examined in future studies on spatial interaction in motion.

The effect of luminance contrast on the mode of motion induction was examined in other studies. Murakami and Shimojo (1993) varied the luminance contrast of random-dot targets. They reported that as luminance contrast increased, motion induction changed from motion assimilation ("motion capture" in their terms) to motion contrast (called "induced motion" in

their study) at moderate eccentricities. The luminance contrast effect appears to contradict the results of the present study. However, the difference in the stimulus configuration could explain the discrepancy; in their study, the inducing random dots were placed not only on the surround area but also on the target area, whereas in the present study the target and the inducer were segregated. The inducer dots superimposed on the target may contribute to motion assimilation of the low-contrast target. It should be also noted that motion capture has often been reported on targets superimposed on the inducers (Ramachandran and Inada 1985; Ramachandran, 1987; Ramachandran and Cavanagh 1987; Yo and Wilson 1992).

Ohtani et al (1995) also examined the effect of luminance contrast on the motion assimilation of two-frame motion. They found that motion assimilation strengthened as the luminance contrast of the inducers increased, but it weakened as the luminance contrast of the target increased. However, motion contrast was not observed at all luminance contrast level. They also showed that their luminance contrast effects could be explained by fixed center-surround interaction with contrast normalization. Thus, their results support the finding that the mode of motion induction is unaffected by luminance contrast, though the magnitude of motion induction may be affected by luminance contrast.

Ohtani et al (1995) and Murakami and Shimojo (1993) varied luminance contrast of center and surround separately, but in the present study the manipulations of luminance contrast were applied to both centre and surround stimuli. Since the ratio of the center contrast to the surround contrast was kept constant for the standard and the low luminance contrast conditions, the contrast manipulation would not be a problem. Paffen et al (2005, 2006) examined center-surround interaction in motion using the target grating ringed by the surround grating in binocular rivalry. They also varied luminance contrast for both center and surround together. Paffen et al. (2006) reported that surround inhibition disappeared at low luminance contrast, while in the present study motion contrast was found even at low luminance contrast. Since Paffen et al. (2006) covaried center and surround contrasts in the same way as it was done here, the discrepancy cannot be attributed to the contrast manipulation.

Center-surround interaction in motion processing has been attributed to the suppression of motion-sensitive cells by surround stimulation (e.g., Nawrot and Sekuler 1990; Murakami and Shimojo 1996). Many cells in V1 have motion direction selectivity and show surround modulation, which is generally inhibitory (e.g., Kapadia et al 1999; Sceniak et al 1999; Cavanaugh et al 2002; Jones et al 2002). Decrease of luminance contrast generally weakens surround inhibition of V1 cells (Kapadia et al 1999; Sceniak et al 1999; Cavanaugh et al 2002). Pack et al (2005) also reported that the surround suppression of many cells in MT weakened with a decrease in the luminance contrast, although surround suppression of some cells strengthened with it. To my knowledge, this is the only study that examined luminance contrast effect on center-surround interaction in MT neurons. Pack et al (2005) employed random-dot stimuli. Luminance contrast effect on surround modulation in MT has not been examined with grating stimuli. Thus, there seems to be less evidence of the contrast modulation of center-surround interaction for MT than for V1. Effects of noise and luminance contrast on motion induction reported in the present study might be attributed to properties of MT neurons. Surround inhibition of neurons in MT may remain constant or become stronger for gratings as luminance contrast decreases, while surround suppression may become weaker as the noise level increases. It would be valuable to examine noise and luminance contrast effect on surround modulation in MT using grating stimuli.

Functional roles of center-surround interactions in motion processing have been discussed in several studies. Allman et al (1985) proposed that center-surround interactions play a role in figure-ground segregation. In addition, they are useful for three-dimensional shape computation (Koenderink and van Doorn 1992). It was also suggested that center-surround interactions reflect the optimization of information transmission. The information-theoretic models predict that, as SNR decreases, the filter characteristic changes from band-pass to low-pass (Atick and Redlich 1990; Atick 1992; van Hateren 1993). The differential effect of noise and luminance contrast reduction on motion induction found in this study implies that motion induction is not necessarily affected by SNR or visibility. Some revisions to information-theoretic approaches to motion processing might be required. Signal intensity is generally defined as luminance contrast, or the power of the signals. This definition may not be valid for motion stimuli. Motion information is extracted from luminance or color information by non-linear processes. Nonlinearity may also arise due to response saturation to luminance contrast. Furthermore, due to the aperture problem, high luminance contrast does not necessarily mean high reliability of motion information. Since signal strength in the motion system may be ill-defined owing to

these non-linear processes and the aperture problem, the motion processing system may rely more on noise level than on luminance contrast for adaptive change of receptive fields. In line with this view, Huang et al (2007, 2008) reported that surround modulation of cells in MT depends on motion ambiguity due to the aperture problem; ambiguous motion due to the aperture problem within the classical receptive field elicits integrative modulation, whereas unambiguous motion elicits antagonistic or no directional modulation. A new framework, including not only luminance contrast and noise, but also the aperture problem and nonlinearity, is required for future theorization.

Acknowledgements

This research was supported by a Grant-in-Aid for Scientific Research (No. 16730367) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

- Aaen-Stockdale C R, Thompson B, Huang P C, Hess R F, 2009 "Low-level mechanisms may contribute to paradoxical motion percepts" *Journal of Vision* **9**(5) 9.1-14
- Allman J, Miezin F, McGuinness E, 1985 "Direction-and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT)" *Perception* **14** 105-126
- Atick J J, 1992 "Could information theory provide an ecological theory of sensory processing" *Network* **3** 213-251
- Atick J J, Redlich A N, 1990 "Towards a theory of early visual processing" *Neural Computation* **2** 308-320
- Barlow H B, Fitzhugh R, Kuffler S W, 1957 "Change of organization in the receptive fields of the cat's retina during dark adaptation" *Journal of Physiology* **137** 338-354
- Born R T, Tootell R B, 1992 "Segregation of global and local motion processing in primate middle temporal visual area" *Nature* **357** 497-499
- Cavanaugh J R, Bair W, Movshon J A, 2002 "Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons" *Journal of neurophysiology* **88** 2547-2556
- Chang J J, Julesz B, 1984."Cooperative phenomena in apparent movement perception of random-dot cinematograms" *Vision Research* **24** 1781-1788
- Churan J, Richard A G, Pack C C, 2009 "Interaction of spatial and temporal factors in psychophysical estimates of surround suppression" *Journal of Vision* **9**(4) 15.1-15
- Duncker K, 1929 "Über induzierte Bewegung" Psychologishe Forschung 12 180-259
- Glasser D M, Tadin, D, 2010 "I Low-level mechanisms do not explain paradoxical motion percepts" *Journal of Vision* **10**(4) 20.1-9

Hanada M, 2004 "Effects of the noise level on induced motion" Vision Research 44 1757-1763

Hateren J H van, 1993 "Spatiotemporal contrast sensitivity of early vision" Vision Research 33 257-267

- Huang X, Albright T D, Stoner G R, 2007 "Adaptive surround modulation in cortical area MT" *Neuron* **53** 761-770
- Huang X, Albright T D, Stoner G R, 2008 "Stimulus dependency and mechanisms of surround modulation in cortical area MT" *The Journal of Neuroscience* **28** 13889-13906
- Ido K, Ohtani Y, Ejima Y, 1997 "Dependencies of motion assimilation and motion contrast on spatial properties of stimuli: spatial-frequency nonselective and selective interactions between local motion detectors" *Vision Research* **37** 1565-1574
- Ido K, Ohtani Y, Ejima Y, 2000 "Summation between nearby motion signals and facilitative/inhibitory interactions between distant motion signals" Vision Research 40 503-516
- Jones H E, Wang W, Sillito A M, 2002 "Spatial organization and magnitude of orientation contrast interactions in primate V1" *Journal of Neurophysiology* **88** 2796-2808
- Kapadia M K, Westheimer G, Gilbert C D, 1999 "Dynamics of spatial summation in primary visual cortex of alert monkeys" *Proceedings of the National Academy of Sciences of the USA* 96 12073-12078
- Koenderink J J, van Doorn A J, 1992 "Second-order optic flow" Journal of the Optical Society of America A 9 530-538
- Levi D M, Schor C M, 1984 "Spatial and velocity tuning of processes underlying induced motion" *Vision Research* **24** 1189-1196
- Murakami I, Shimojo S, 1993 "Motion capture changes to induced motion at higher luminance contrasts, smaller eccentricities, and larger inducer sizes" *Vision Research* **33** 2091-2107
- Murakami I, Shimojo S, 1996 "Assimilation-type and contrast-type bias of motion induced by the surround in a random-dot display: evidence for center-surround antagonism" *Vision Research* 36 3629-3639
- Nawrot M, Sekuler R, 1990 "Assimilation and contrast in motion perception: explorations in cooperativity" *Vision Research* **30** 1439-1451
- Nishida S, Edwards M, Sato T, 1997 "Simultaneous motion contrast across space: involvement of second-order motion?" *Vision Research* **37** 553-563

- Ohtani Y, Ido K, Ejima Y, 1995 "Effects of luminance contrast and phase difference on motion assimilation for sinusoidal gratings" *Vision Research* **35** 2277-2286
- Over R, Lovegrove W, 1973 "Color-selectivity in simultaneous motion contrast" *Perception & Psychophysics* 14 445-448
- Pack C C, Hunter J N, Born R T 2005 "Contrast dependence of suppressive influences in cortical area MT of alert macaque" *Journal of Neurophysiology* **93** 1809-1815
- Paffen C L E, Tadin D, Pas S F te, Blake R, Verstraten F A J, 2006 "Adaptive center-surround interactions in human vision revealed during binocular rivalry" *Vision Research* **46** 599-604
- Paffen C L, Smagt M J van der, Pas S F te, Verstraten F A, 2005 "Center-surround inhibition and facilitation as a function of size and contrast at multiple levels of visual motion processing" *Journal of Vision* 5 571-578
- Ramachandran V S, 1987 "Interaction between colour and motion in human vision" *Nature* **328** 645-647
- Ramachandran V S, Inada V, 1985 "Spatial phase and frequency in motion capture of random-dot patterns" *Spatial Vision* **1** 57-67

Ramachandran V S, Cavanagh, P, 1987 "Motion capture anisotropy" Vision Research 27 97-106

- Ryan T A, 1959 "Multiple comparisons in psychological research" Psychological Bulletin 56 26-47
- Sceniak M P, Ringach D L, Hawken M J, Shapley R, 1999 "Contrast's effect on spatial summation by macaque V1 neurons" *Nature Neuroscience* 2 733-739
- Tadin D, Lappin J S, 2005 "Optimal size for perceiving motion decreases with contrast" *Vision Research* **45** 2059-2064
- Tadin D, Lappin J S, Gilroy L A, Blake R, 2003 "Perceptual consequences of centre-surround antagonism in visual motion processing" *Nature* **424** 312-315
- Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E, 1986 "Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey" *Journal of Neuroscience* 6 134-44

Yo C, Wilson H R, "Moving two-dimensional patterns can capture the perceived directions of lower or higher spatial frequency gratings" *Vision Research* **32** 1263-1269

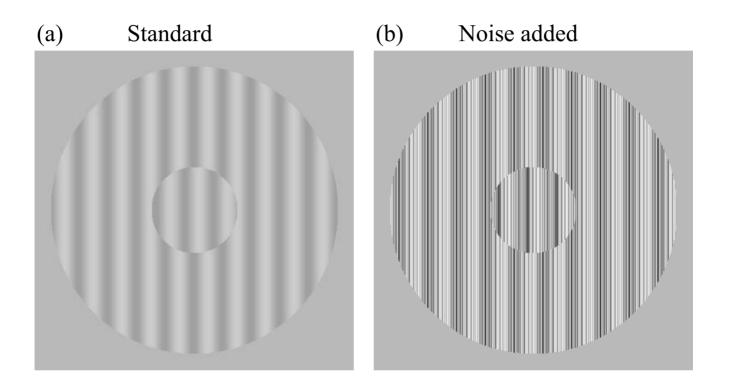


Figure 1

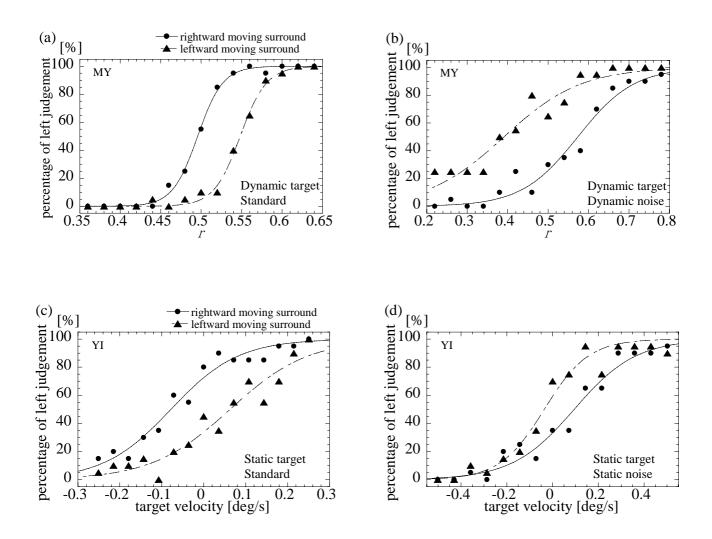


Figure 2

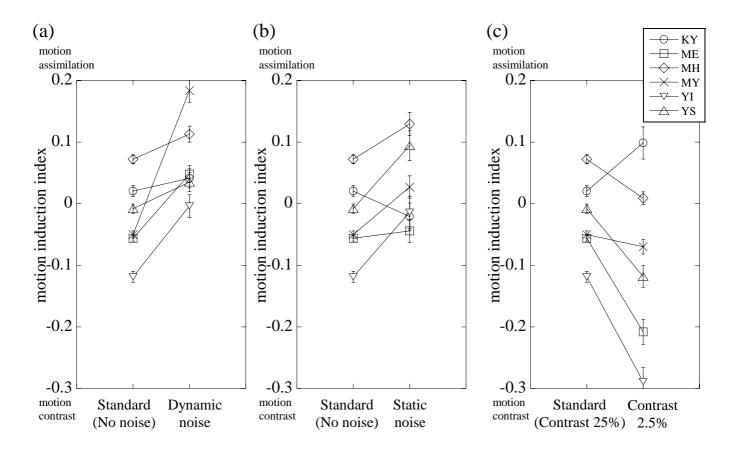


Figure 3

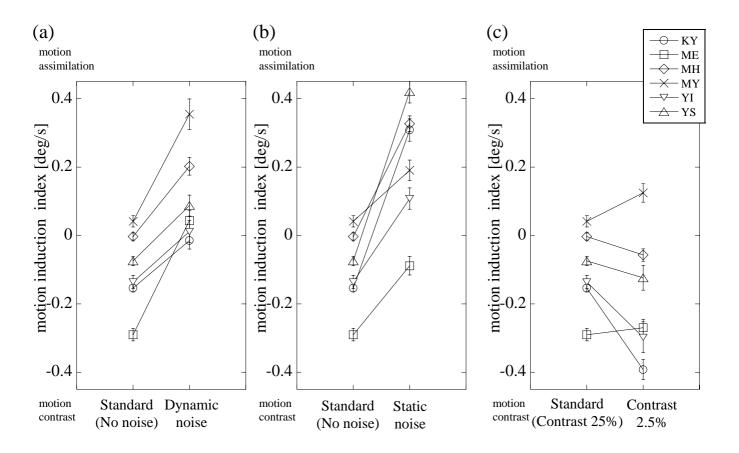


Figure 4

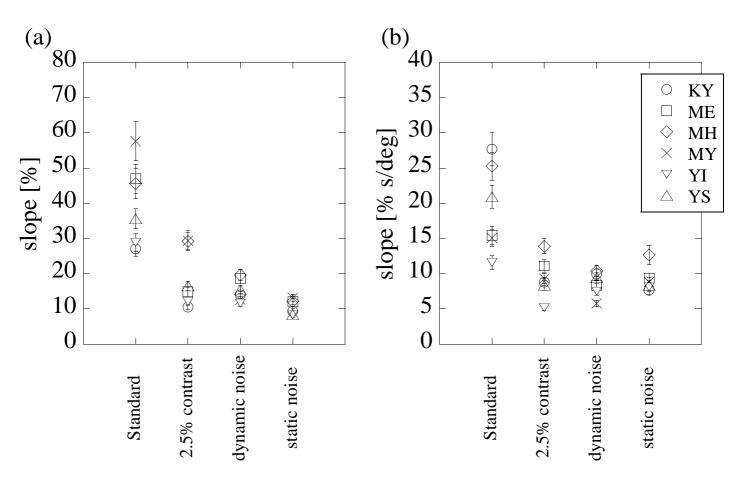


Figure 5

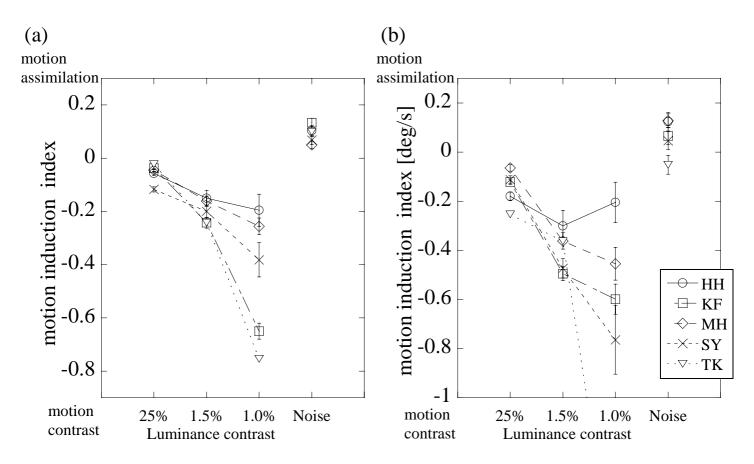


Figure 6

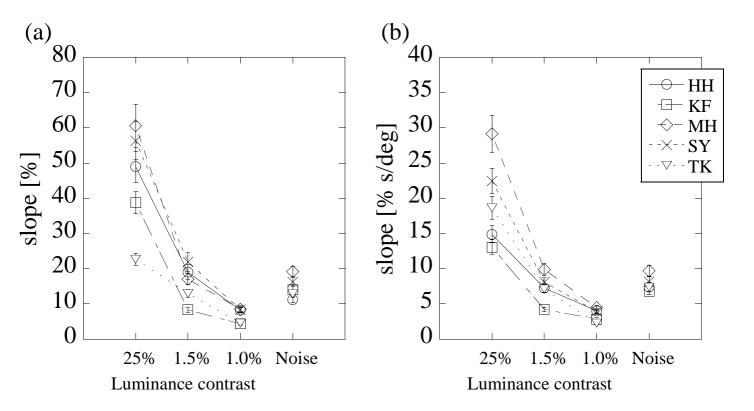


Figure 7